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THE WINGS OF INSECTS.

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CHAPTER I.

An Introduction to the Study of the Homologies of the Wing-Veins.

It is the purpose of this series of papers to present a summary of what is known regarding the structure and development of the wings of insects, to give the results of some investigations in these fields made by the writers, and to indicate the value in taxonomic work of the characters presented by the wings.

As the growth of our knowledge naturally proceeds from a study of the obvious facts of nature to those that are more deeply hidden, it seems best to discuss first the structure of the wings of adult insects and to postpone for a time the study of the beginnings of wings. It will be necessary, however, to take up early in the discussion a study of the structure of the wings in those stages that immediately precede the adult stage, the pupæ of insects with a complete metamorphosis, and the nymphs of insects with an incomplete metamorphosis. It is in this field that we have the most to offer that is new.

Several writers have appreciated the fact that much light can be thrown on the problem of determining the homologies of the wing-veins by a study of the tracheæ that precede them in the wings of immature insects. The more important of the contributions that have been made to this phase of the question are those of Brauer and Redtenbacher¹ and of Spuler.² Still, comparatively little has been done in this direction.

This is doubtless due to the difficulties that have stood in the way of work of this kind. The tracheæ of the wings of pupæ and nymphs are often very delicate, and when filled with

¹ Brauer und Redtenbacher, Ein Beitrag zur Entwicklung des Flügelgeäders der Insecten. *Zool. Anz.*, 1888, pp. 443-447.

² A. Spuler, Zur Phylogenie und Ontogenie des Flügelgeäders der Schmetterlinge. *Zeit. f. wiss. Zool.*, Bd. liii, 1892, pp. 597-646.

the medium in which a wing is mounted for microscopic study they are usually invisible. It is not strange, therefore, that they have been studied so little. But in the course of our investigations we have devised a method of study of the wings of immature insects which renders the observation of the tracheæ in them a simple matter.

If a living pupa or nymph be placed in formol (4%) the tissues of the wings will be rendered translucent in a short time. In the case of very delicate insects only a few hours

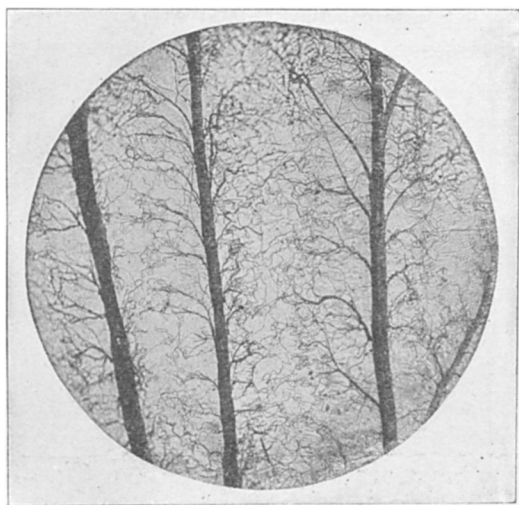


FIG. 1. — Part of a wing of a pupa of *Corydalis cornuta*.

are required for this, but with larger ones with more opaque wings it is necessary to leave them in the formol for several days, or even for several weeks. While the formol renders the tissues translucent, it does not soon penetrate the tracheæ, which are, therefore, left filled with air, and appear as dark lines when the wing is examined with transmitted light. Just after molting some wings are translucent, but there are few so clear that a short stay in formol will not make them clearer.

In order to study wings prepared in this way, they are removed from the body and mounted in glycerine jelly, care being taken to cool the mount quickly so that the jelly will not

penetrate the tracheæ. In this way most beautiful objects can be prepared, which will show the minutest ramifications of the tracheæ.¹ Fig. 1 is a half-tone reproduction of a photograph of an object prepared in this way. This figure represents a small portion of a wing of a pupa of *Corydalis cornuta*.

Not only can the tracheæ that precede the wing-veins be studied in this manner, but, if the wing be taken at the right stage, the cuticular thickenings destined to form the wing-veins, as well as their corresponding tracheæ, if there be any, can be seen. Figs. 2 and 3 are half-tone reproductions of photographs of wings taken at this stage.

There is, however, one undesirable feature of preparations made in this manner; it is that after a time the cuticular thickenings become indistinct, and the glycerine jelly will penetrate the tracheæ, rendering all except the larger ones invisible. But as it is a very easy matter to photograph such preparations, and as a series of photo-micrographs are much more easily compared than a series of microscopic slides, this feature does not materially impede an investigation of this kind. Usually the cuticular thickenings show best as soon as a mount is made, while the tracheæ stand out more sharply twenty-four hours after mounting, because of the clearing effect of the glycerine jelly upon the cuticular parts. It is, therefore, frequently desirable to make, at different times, two or more photographs of the same specimen.

¹ In making mounts of this kind our usual procedure was to spread a drop of melted glycerine jelly on a slide and allow it to cool; then to dissect off the wings (generally under water), taking with them just enough of the thorax to include the basal attachments of the tracheæ; then to place these wings upon the solidified glycerine jelly on the slide; then to lower upon the wings a heated cover glass, causing the jelly to melt enough to envelope the wings; and then to cool the mount speedily on a cake of ice, a marble slab, or in a draught of cold air. Rapid cooling is imperative, for in melted glycerine jelly the tracheæ soon become filled, and the smaller ones are then invisible.

It is imperative, also, that the wings be handled with care. Being simple sac-like structures, the tracheæ are almost free within them, and a slight pinch with forceps in the middle of the wing may throw all of its tracheæ out of place. It is better to lift the wing by its thoracic attachments or upon a section lifter.

Not every pupal wing is fitted for this study. Just before molting, and especially just before the last molting, the wing becomes so crumpled within its old sheath that the course of its tracheæ can be followed only with difficulty. Much time can be saved by the selection of the paler individuals for study.

It is obvious that one who has learned the homologies of the principal tracheæ of wings can easily determine the homologies of the wing-veins of the adult by the study of wings taken in the stage of development shown by Figs. 2 and 3. It should be remembered, however, that the determining of the homologies of these tracheæ necessitates the study of a large series of well-selected types. One is not warranted in arriving at conclusions in this matter from the study of a few representatives of a single order of insects.

During the past year we have studied in the manner indicated the wings of representatives of nearly all of the more important groups of winged insects, and have made several

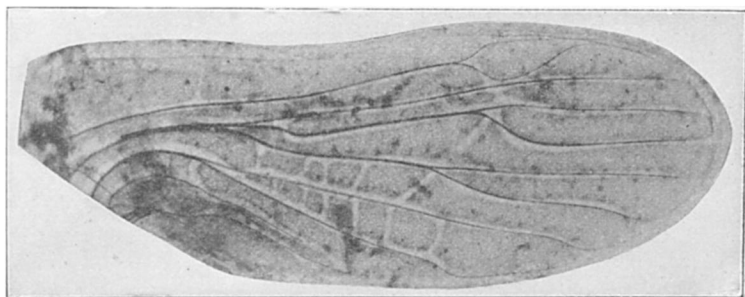


FIG. 2. — Fore wing of a nymph of *Nemoura*.

hundred photo-micrographs of them. We feel, therefore, that we have at hand sufficient data to warrant the conclusions regarding the homologies of the wing-veins that we purpose to offer.¹

Although Figs. 2 and 3 will be discussed in detail in a subsequent chapter, we will give a few words of explanation here. These figures represent the wings of one side of a nearly mature nymph of a *Nemoura*, one of the genera of stone flies (Plecoptera). In making the preparations it was impracticable to remove all of the dirt adhering to the wings without danger of injuring them; this is often the case in preparing mounts of

¹ The most important gap in our series of observations is due to the fact that as yet we have been unable to procure pupæ of any of the Mecoptera. We would, therefore, be under great obligations to any one who would send us living pupæ of either *Panorpa* or *Bittacus*.

the wings of aquatic nymphs. The irregular blotches of dark color in the figures are due to this cause. The dark lines traversing the disk of the wing represent the tracheæ, and the pale bands the cuticular thickenings destined to form the wing-veins.

It will be observed that the principal veins are formed along the courses of tracheæ, while in most cases the cross-veins have no tracheæ within them. It will also be observed that the tracheæ extend in straight lines or in gentle curves, while in some cases the corresponding veins are much more angular.

It is evident from this that in the perfecting of a wing as an organ of flight the position of a vein in the adult may become

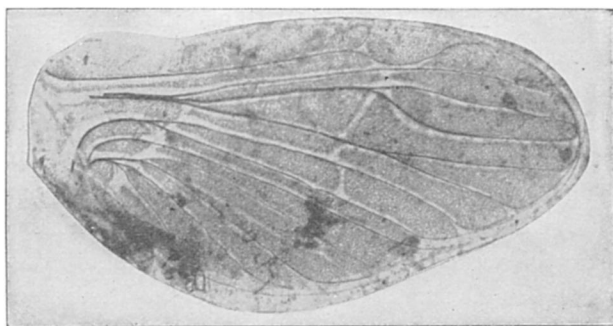


FIG. 3. — Hind wing of a nymph of *Nemoura*.

quite different from that of the corresponding trachea of the immature form. In other words, although there is no doubt that the courses of the principal wing-veins of primitive insects were determined by the position of the principal tracheæ of the wings, the wing-veins have been more or less modified to meet the needs of adult life; while at the same time the tracheæ of the immature wing, serving the purpose of respiration, and lying more or less free within the wing-sac, have not been forced to follow closely the changes in the cuticular thickenings of that sac.

The operation of this principle is shown only to a slight extent in the wings figured here. But when we study more highly specialized forms, it is seen that the divergence of these

two sets of structures is sometimes very wide, and must be taken into account in an interpretation of the characters presented by a wing.

While this increases the difficulty of determining the homologies of the wing-veins, it is often of great aid in taxonomic work, for it may afford an indication of the degree of divergence from a primitive type in the structure of a wing; and when a series of forms is studied the course of this divergence is often clearly indicated.

The figures also show that in some cases what appears as a single vein is formed about two closely parallel tracheæ. This is shown in the case of the bases of the second and third principal tracheæ, counting from the costal margin of the wing, the radial and medial tracheæ. This illustrates a fact of frequent occurrence, — that what appears to be a single vein may be formed by the coalescence of two primitive veins.

In these figures the tracheæ just mentioned, except one of them in the fore wing, appear not to extend to the base of the wing. This is due to the fact that in the preparations photographed the mounting medium had penetrated these tracheæ for a distance, rendering the basal portion of them invisible.

The figure of the hind wing illustrates also another way in which specimens may be injured during their preparation, and which may lead to a misinterpretation of them. In this wing the first branch of the first main trachea, the subcostal trachea, has been broken and moved out of place within the wing-sac. The normal position of this branch is well shown in the figure of the fore wing.

We will not go farther into the discussion of the technique of this method of study. Enough has been said to show that we have at hand a comparatively simple method of determining those questions of homologies of wing-veins that have sorely puzzled all investigators that have attempted to deal with them, and to indicate the nature of the material upon which we have based the conclusions that we purpose to offer in succeeding chapters of this paper.